Water Budget in Some Populations of the European Common Lizard, Lacerta vivipara Jacquin
Author(s): C. Grenot, B. Heulin, T. Pilorge, M. Khodadoost, A. Ortega and Y.-P. Mou
Reviewed work(s):
Source: *Functional Ecology*, Vol. 1, No. 2 (1987), pp. 131-138
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/2389716
Accessed: 08/06/2012 15:55

Functional Ecology 1987,
1, 131-138

Water budget in some populations of the European common lizard, *Lacerta vivipara* Jacquin

C. GRENOT*, B. HEULIN†, T. PILORGE*, M. KHODADOOST*, A. ORTEGA‡§ and Y.-P. MOU*
**Centre National de la Recherche Scientifique U.A. 258, Laboratoire d' Ecologie, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France, †Station biologique de Paimpont, 35380 Plélan le Grand, France and ‡Instituto de Ecologia, A.C., Apartado Postal 18-845, Deleg. Miguel Hidalgo, 11800 México D.F., México*

Abstract. The water budget of the lizard *Lacerta vivipara* Jacquin was studied in one lowland and two montane field populations using tritiated water. In all cases, gravid adult females had lower water fluxes and turnover rates than males and yearlings; in the lowland population there were also differences between adult and yearling gravid females. When weighted for egg mass, gravid yearling females did not show any significant difference in water fluxes with non-gravid yearling females. Water flux rates were positively related to the humidity of the biotope. Negative correlations exist between water flux rates and lizard mass and these are probably related to the decrease of the surface:volume ratio as body size increases. Positive correlations exist between flux differences and growth rates, demonstrating that water needs are related to energetic requirements, especially those concerned with growth and activity.

Key-words: Field ecophysiology, *Lacerta vivipara*, lizard, metabolism, tritium, water budget

Introduction

The availability of water in a habitat can greatly influence the animals living in it. Using a labelled isotope technique (Nagy, 1982, 1983; Buscarlet & Grenot, 1985) this study reports the rates of water turnover in free-ranging adult and yearling lizards in several populations of *Lacerta vivipara* Jacquin. This is a small, live-bearing, lacertid lizard (40–60 mm snout–vent length (SVL) in adult males, 47–75 mm SVL in adult females, with an average weight of 3·5–4·0 g in both sexes). It is widely distributed in Europe and Asia, especially in the most northern regions and under relatively harsh climates for an ectothermic species (Arnold, 1973; Arnold, Burton & Ovenden, 1978). Although it seems to prefer humid biotopes, it is found in varying physical environments (especially vegetation and soil moisture).

Measurements were made for several age and sex categories, and field water budgets are presented in relation to the population biology of one lowland (Heulin, 1985a, b, c, 1986) and two montane populations (Khodadoost, Pilorge & Ortega, 1987; A. Ortega, T. Pilorge & M. Khodadoost, unpublished; Pilorge, 1987).

The following issues were examined:

(1) Are water turnover rate and body mass negatively related in *L. vivipara* (Peters, 1983)?

(2) Is the water budget influenced by sex and age?

(3) Are there seasonal changes in water budgets?

(4) Are water budgets influenced by reproductive status in females?

(5) Do water budgets differ between populations according to the degree of humidity of the biotope?

Other studies of water relationships in lizards include: Bradshaw (1981); Congdon *et al.* (1982); Lemire, Grenot & Vernet (1982); Nagy, Huey & Bennett (1984); Vernet, Grenot & Nouira (1986); Vernet, Lemire & Grenot (1987); and see reviews in Minnich (1979) and Nagy (1982).

Study areas

The lowland population studied here is situated at Paimpont (Brittany, France, hereafter designated as BLA; Table 1). The herbaceous vegetation was largely dominated by *Molinia coerulea* (L.) Moench. Because of its location on the banks of a

---

* §Present address: Centro de Investigaciones Biologicas de Baja California Sur, Apartado Postal 128, La Paz, 23060, B.C.S., México.

lake peat bog, the soil was usually saturated with water. In this population, a variable proportion of females reproduced when only one year old (Heulin, 1985a).

The other two populations are situated on Mont Lozère (France) at similar altitudes (Mas de la Barque is referred to as CMB and Chalet du Mont Lozère as CCML). The biotope at CMB was a heathland where *Calluna vulgaris* (L.) Hull was the dominant cover. In contrast, the largely herbaceous vegetation at CCML was dominated by *Nardus stricta* L., *Festuca rubra* L., and *Deschampsia flexuosa* (L.) Trin. Low shrubs were mainly represented by *C. vulgaris*. Soil water contents were noticeably lower at both CMB and CCML than at BLA (Table 1). In these two populations, females did not reproduce until they were 2 or even 3 years old (Bauwens, Heulin & Pilorge, 1987).

During the experiments, shade air temperature and relative humidity were recorded (Table 2).

Materials and methods

Lizards were sampled on one or two successive days. The precise location of each capture was marked with a stick. Lizards were identified, marked by toe-clipping and paint markings were placed on their backs. The specimens were weighed to the nearest milligram with an electronic, portable balance and injected intraperitoneally with 0·010–0·040 ml of water containing ^{3}H at 9·7 MBq ml^{-1} and 97 atoms ^{18}O per 100 atoms total oxygen. Total body water was estimated by dilution of the injected isotope ^{3}H (required for calculating H_2O fluxes) after equilibration. Preliminary tests showed that there was no apparent difference between results given by plasma or urine samples; thus, urine samples were preferred. After equilibration for 3–5 h, liquid urine samples were collected from the cloaca. Lizards were then released at the point of capture, left undisturbed for 3–8 days and then recaptured.

Those recaptured were reweighed and their cloacal urine sampled again. The volumes of urine collected in this way were sufficient to determine accurately ^{3}H activity by liquid scintillation spectrometry. Total water influxes and effluxes were calculated based on the reduction in ^{3}H activity, the original body water content and assuming that changes in body mass were linear (Nagy & Costa, 1980). Additional lizards were autopsied and their sex, reproductive condition (females) and body and egg water contents determined. Water content was calculated as the difference between live and oven dry (80 °C) masses divided by live mass. The average body

Table 1. Main physical and vegetational features of the three biotopes. ++ = low; +++ = medium; +++++ = high.

	CMB	CCML	BLA
Elevation (m)	1425	1410	150
Exposure	south	north	west
Slope	2%	15%	0%
Vegetation:			
average height (cm)	30–35	20–25	35–60
global cover:			
low shrubs	80%	30%	15%
herbaceous plants	40%	80%	90%
floristic richness (# determined species)	55	48	46
Soil:			
water	+++	++	+++++
depth (cm)	60–100	60–100	50–70

Table 2. Minimum, maximum and average temperatures (°C) and air humidity (%) in the three populations during the period of study in July 1985.

	Temperature			Air humidity		
	Minimum	Maximum	Average	Minimum	Maximum	Average
BLA	7·5	29·0	17·3 ± 6·2	36·5	98	74·8 ± 23·6
CMB	6·0	28·0	14·3 ± 8·1	45	95	75·8 ± 19·5
CCML	7·5	28·5	16·0 ± 6·8	50	99	79·7 ± 19·4

water content of lizards autopsied at the time of injection did not differ noticeably from that of animals recaptured 3–8 days later.

This experiment was conducted in June 1984, July 1985 and September 1985 at BLA and in July 1985 at CMB and CCML.

Twenty lizards were captured at BLA in July 1985 and kept in individual terraria in the laboratory. Room temperature was held between 19·7 ± 2·8°C during the night and 28·0 ± 2·2°C in the daytime. Additional heating was provided for 8 h per day by a light bulb (60 W) placed above each terrarium. Water was given in small Petri dishes and lizards were fed on young locusts. In order to estimate the proportion of water provided by food, locusts that were not consumed were weighed and the amount ingested by lizards was calculated from the difference between the mass of prey offered and the mass of those not eaten.

The three parameters considered were water influx (WIF), water efflux (WEF) and water turnover rate, *k*. Lizards of each population were divided into four categories: yearlings, adult non-gravid females, gravid adult females and adult males. A fifth category, gravid yearling females, was identified in the BLA population in July 1985 in the field. Eggs are almost totally impermeable to maternal water fluxes, especially in the final stages of gestation (Xavier & Gavaud, 1987). Thus, in order to eliminate egg mass in the evaluation of water fluxes in and out of the body of the mother, a correction factor (ratio of total lizard mass, including eggs, to somatic lizard mass, excluding eggs) was calculated (Table 3). Comparisons among populations, among lizard categories within the same population and among periods for BLA, for each parameter were tested using *k*-sample, Kruskal-Wallis one-way analyses of variance. Where comparisons were significant, samples were compared using pairwise, Mann and Whitney *U*-tests (Siegel, 1956). Comparisons were also made between the results obtained in the field and those calculated from laboratory data at BLA in July 1985. An overall comparison among the three population samples was conducted, involving all the values of WIF and WEF, using Kendall's coefficient of concordance test. All statistical tests were considered significant when $P < 0{\cdot}05$.

Linear regression analyses were needed to examine the relationships between lizard mass and water flux and turnover rates, between relative growth in mass per time unit and water fluxes, and between relative growth in mass and the difference between influxes and effluxes.

Results

In the three populations that were studied, water fluxes of gravid females were approximately half those of non-gravid females (Table 4). At BLA in July 1985, gestation was less advanced in gravid yearlings (stage 23–27, Dufaure & Hubert, 1961) than in gravid adult females (stage 35–40); on the other hand, gravid yearlings had higher water fluxes and turnover rates than gravid adult females (Table 4). When adjusted for egg mass, the water fluxes of gravid yearling females were similar to those of non-gravid yearling females (Table 4).

There were significant differences between all categories of lizards in the two montane populations (Table 5). In the lowland population (BLA) in June 1984 and July 1985, water fluxes and turnover rates increased in the order: (1) gravid adult females; (2) gravid yearling females; (3) males and the other yearlings. There was no significant difference between males and non gravid yearlings (Tables 4 and 5). In September 1985 at BLA, none of the parameters considered differed significantly between the various groups of lizards. Water flux rates and turnover rates for this period showed a considerable decrease with regard to July 1985. It is also worth noting that water fluxes and turnover rates of males in the laboratory were about half those in the field (Table 5) at the BLA site.

Linear regression analyses showed that there were significant negative relationships between WIF and WEF and the average body masses of

Table 3. Average coefficients used to weight gravid female fluxes and turnover rates for egg mass. July 1985 L was conducted in the laboratory; ad = adults; yrl = yearling.

			BLA			
					July 1985	
	CMB	CCML	June 1984	July 1985 L	ad	yrl
$\bar{x}$	1·64	1·54	1·30	1·92	1·91	1·50
SD	0·17	0·10	0·07	0·17	0·13	0·07
n	5	7	3	3	10	4

Table 4. Comparison of water influxes and effluxes in gravid (G) and non-gravid (N-G) females in each population. Corrected values are weighted for egg mass in gravid females. WIF = water influx; WEF = water efflux; k = water turnover rate. Average values are given ±1 SE, except for the corrected figures of gravid females for which the proportion of egg mass in total body mass was not available for the experimental individuals. Sample sizes are indicated in parentheses.

	WIF ($\text{ml kg}^{-1}\text{ day}^{-1}$)		WEF ($\text{ml kg}^{-1}\text{ day}^{-1}$)		k (day^{-1})	
	G	N-G	G	N-G	G	N-G
CMB July 1985	(6)	(3)	(6)	(3)	(6)	(3)
	106·0	220·6	110·0	194·4	13·1	29·2
	±30·4	±24·1	±24·5	±20·1	±3·8	±3·2
corrected	173·8		180·4			
CCML July 1985	(6)	(3)	(6)	(3)	(6)	(3)
	87·1	186·0	89·7	175·6	10·7	24·6
	±21·0	± 7·4	±20·8	± 9·4	±2·6	±1·0
corrected	134·1		138·1			
BLA						
June 1984	(4)	(6)	(4)	(6)	(4)	(6)
	139·4	256·6	131·0	247·4	19·1	34·0
	±15·2	±27·4	±12·6	±34·6	±2·1	±3·6
corrected	181·2		170·3			
July 1985	(4)	(4)	(4)	(4)	(4)	(4)
yearlings	169·5	254·4	163·8	252·7	23·3	34·3
	±17·2	±52·6	±18·0	±47·7	±2·3	±7·1
corrected	254·3		245·7			
July 1985	(10)		(10)		(10)	
Adults	100·8		103·4		12·7	
	±19·2		±18·2		±2·2	
corrected	192·5		197·5			
Lab July 1985	(4)	(3)	(4)	(3)	(4)	(3)
	88·2	238·8	94·6	234·1	11·2	32·2
	±37·3	±37·6	±41·2	±46·9	±4·9	±5·0
corrected	169·3		181·6			

individuals (Table 6). In contrast, there were no significant relationships between these fluxes and relative growth rate in live mass per unit of time ($\text{ml.g}^{-1}\text{ day}^{-1}$). However, in all cases there were highly significant, positive correlations between the difference WIF-WEF and relative growth rates per day (Table 7).

Discussion

Here, in turn, we shall consider the five questions asked in the introduction.

Influence of body mass on water budget

As expected, there were significant negative relationships between water flux rates and body mass (cf. Nagy, 1982). However, in spite of negative, though not significant, correlations between water flux rates and relative growth rates, there were strong positive correlations between the difference between WIF and WEF (= dF) and relative growth rate. Thus, water fluxes decreased when body mass and relative growth rate increased; in contrast, the water retained in the body increased as growth rate increased. These results suggest that a high water turnover rate is incompatible with the retention of a large amount of water in the body. The strong correlation between the energetic investment in growth and the amount of water retained in the body of the lizard implies that water is mainly provided by food. However, the dietary water in the locusts consumed by lizards kept in the laboratory made up only 7–29% of the total WIF (Table 8). As the water content of the prey found by the lizards in nature was very similar to that of the locusts given in the laboratory (Avery, 1971), this should also be true in the field. Hence, there appears to be no direct causal relationship between dF and relative growth rate. Of course, both will be influenced by the high level of metabolism that occurs in smaller, fast-growing lizards (Heulin, 1984; Pilorge, 1982, and unpublished data).

Influence of age and sex on water budget

Even though the differences between yearlings and males were not significant at BLA, the general trend in the level of water fluxes and turnover rates appeared to follow the order:

(non-gravid) yearlings > males > gravid yearling females > adult gravid females.

As already noted, yearlings, especially non-gravid ones, invested the greatest possible part of the ingested energy in growth, while adult males expended more energy in movement over a greater home range than other lizard categories (Heulin,

Table 5. Values of water influxes, effluxes and water turnover rates in the three populations in July 1985 and at various periods of study at BLA. ♀ G = gravid females; ♂ = males; ad = adults; yrl = yearlings. WIF, WEF and *k* are expressed in the same units as in Table 4. Average values are given ±1 SE.

Population and period	Sex	*n*	WIF	WEF	*k*
CMB	♀ G	6	106·0 ± 30·4	110·0 ± 24·5	13·1 ± 3·8
	♂	4	173·1 ± 19·5	155·5 ± 21·6	23·7 ± 2·7
	yrl	7	272·5 ± 56·9	241·4 ± 51·4	36·2 ± 7·6
CCML	♀ G	6	87·1 ± 21·0	89·7 ± 20·8	10·7 ± 2·6
	♂	4	142·7 ± 27·8	134·5 ± 26·6	19·6 ± 3·8
	yrl	4	191·8 ± 11·8	179·3 ± 10·4	25·4 ± 1·6
BLA					
June 1984	♀ G	4	139·4 ± 15·2	131·0 ± 12·6	19·1 ± 2·1
	♂	7	234·1 ± 47·3	244·4 ± 48·9	31·1 ± 6·3
	yrl	11	258·7 ± 35·5	252·1 ± 37·6	34·3 ± 4·7
July 1985	♀ G yrl	4	169·5 ± 17·2	163·8 ± 18·0	23·3 ± 2·3
	♀ G ad	10	100·8 ± 19·2	103·4 ± 18·2	12·7 ± 2·2
	♂	5	242·2 ± 25·1	241·0 ± 18·0	33·2 ± 3·5
	yrl	6	268·5 ± 60·3	267·9 ± 58·2	36·2 ± 8·1
July 1985 lab	♀ G ad	4	88·2 ± 37·3	94·6 ± 41·2	11·2 ± 4·9
	♂	6	136·2 ± 14·2	141·5 ± 14·5	18·9 ± 2·0
	yrl	6	228·6 ± 37·6	225·3 ± 39·9	30·8 ± 5·0
September 1985	♀	3	113·3 ± 16·3	99·2 ± 22·1	15·3 ± 2·2
	♂	2	83·8 ± 7·7	79·9 ± 0·3	11·5 ± 0·7
	yrl	5	97·7 ± 14·8	93·2 ± 15·3	13·3 ± 1·9

Table 6. Parameters of the linear regression equations relating water fluxes (ml kg^{-1} day^{-1}) to the average weight of the individual (g) during the experiment. *n* = sample size. All correlation coefficients are significant at $P < 0\cdot05$.

	WIF = f(W)				WEF = f(W)		
	r	*b*	*a*	*n*	*r*	*b*	*a*
CMB July 1985	0·75	−44·13	347·46	17	0·63	−29·79	290·87
CCML July 1985	0.73	−21·87	234·10	14	0·69	−18·96	219·68
BLA							
June 1984	0·72	−33·30	309·14	19	0·66	−33·23	308·90
July 1985	0·83	−38·31	331·71	25	0·83	−37·24	327·20
September 1985	0·75	−28·54	186·71	9	0·66	−25·11	168·64

Table 7. Parameters of the linear regression equations relating the difference between fluxes (dF = WIF−WEF) to the relative growth rate (day^{-1}) of the individual during the experiment. All correlation coefficients are significant at $P < 0{\cdot}001$.

	dF = f(dW/Wt)			
	r	*b*	*a*	*n*
CMB				
July 1985	0·974	779·35	−3·54	17
CCML				
July 1985	0·964	1044·91	−3·05	14
BLA				
June 1984	0·996	755·87	−0·73	19
July 1985	0·998	725·03	−0·36	25
September 1985	0·956	670·67	0·97	9

1984; Ortega *et al.*, unpublished). By contrast, gravid females exhibited much less locomotory activity than males.

Hence both intensity of activity and growth are likely to influence the rate of water turnover in *L. vivipara*, a conclusion that is supported by the considerable reduction of water flux rates observed in males, compared to that of gravid adult females and yearlings, under laboratory conditions. In these circumstances activity (personal observation) but not growth was reduced.

Seasonal changes

In all categories of lizard at BLA, there were significant decreases in water fluxes and turnover rates in September, just prior to hibernation, compared to June and July. Such a decrease was probably due to a reduction in growth and movement at the end of the activity season. In fact, growth and male locomotory activity were maximum from early June to the end of July, while in September a reduction of metabolism was responsible for a decrease of growth and activity (Xavier & Gavaud, personal communication).

Influence of reproductive status on female water budget

Adult gravid females exhibited the lowest water fluxes and turnover rates of all categories, even when weighted for egg mass. The water flux rates of gravid yearling females were also low but were higher than those of adult gravid females. Moreover, when weighted for egg mass, the water flux rates of gravid yearling females were equivalent to those of other yearlings.

From these results and the conclusions presented in the previous sections, we infer that age, correlated with growth rate, may have a significant influence on water budget. However, in the case of gravid females, differences in the relative importance of clutch mass (Table 3) with age may also contribute to the differences observed in water balance between yearling and adult gravid females.

Comparison between populations

Comparison of the three populations in July 1985 (Kendall's coefficient of concordance test) show that water fluxes were greater in the BLA population than in the other two, and greater at CMB than at CCML. However, the BLA and CMB populations only differed in the water budget of males, while at CCML, all groups had lower water fluxes than at BLA and at CMB. Hence, water flux rates co-vary with soil water content. However, it is likely that soil water content only reflects the amount of water available to lizards in the form of rain and dew.

Such correlations suggest that water balance in *L. vivipara* may be controlled by environmental factors. However, an alternative possibility is that populations may have diverged genetically for these traits. The results of Kobayashi, Mautz & Nagy (1983), on evaporative water loss rates in

Table 8. Amount of water supplied in the food ingested under laboratory conditions in July 1985 for samples of BLA lizards, and proportion of this amount in the total water influx. W = average weight of the lizards during the experiment; FC = food consumption; WF = water content of the food; WF:WIF is the proportion of the total water influx provided by food (the extremes of the range are indicated in parentheses). Means are given ±1 SE.

	n	W (g)	FC	WF ($ml\ kg^{-1}\ day^{-1}$)	WIF	WF:WIF (%)
yrl	6	2·09 ± 0·35	62·4 ± 14·3	44·9 ± 8·7	228·6 ± 41·2	19·6 (13·4 − 28·6)
♂	5	3·49 ± 0·30	31·0 ± 15·9	21·7 ± 11·1	138·4 ± 16·1	15·7 (6·9 − 26·8)
♀G	3	3·56 ± 1·06	31·2 ± 7·5	21·8 ± 5·2	109·2 ± 11·5	20·0 (13·8 − 27·6)

Anolis carolinensis Voigt also raise this problem and stress the role that habitat aridity may play.

Conclusion

It is difficult to compare our results with other field studies on lizards because most have been conducted in arid regions (Bradshaw, 1981; Grenot, 1981; Vernet, Grenot & Nouira, 1986; Vernet, Lemire & Grenot, 1987; and references in Minnich [1979] and Nagy [1982]), tropical forest or coastal habitats. Moreover, the results presented in this study show that water flux and turnover rates vary on a large scale, depending on sex, age, reproductive condition, time of the season and even on the population studied. For example, WIF ranges from about 80 ml kg^{-1} day^{-1} in males in September 1985 at BLA to more than 270 ml kg^{-1} day^{-1} in subadults in July 1985 at CMB. Obviously, any attempt to compare these results with other studies, not taking into account such sources of variation, would be inappropriate (e.g. Nagy, 1982).

Clearly, thorough studies of field water budgets are urgently needed, especially in temperature lizard species but also in other species inhabiting arid or humid tropical habitats.

Acknowledgments

We are greatly indebted to Jean Clobert and to Alister Spain whose comments and criticisms were very helpful. This work was supported financially by the ATP no. 960088 and by the GRECO no. 130082 of the Centre National de la Recherche Scientifique.

References

Arnold, E.N. (1973) Relationships of the paleartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bulletin of the British Museum Zoology,* **25,** 291–366.

Arnold, E.N., Burton, J.A. & Ovenden, D.W. (1978) *Tous les Reptiles et Amphibiens d'Europe en couleurs.* Elsevier Séquoia, Paris.

Avery, R.A. (1971) Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology,* **40,** 351–365.

Bauwens, D., Heulin, B. & Pilorge, T. (1987) (ed.) Variations spatio-temporelles des caractéristiques démographiques dans et entre populations du lézard *Lacerta vivipara.* In *Actes du colloque Biologie des Populations*, pp. 531–536. Centre National de la Recherche Scientifique, Lyon.

Bradshaw, S.D. (1981) Ecophysiology of Australian desert lizards: studies on the genus *Amphibolurus.* In *Ecological Biogeography of Australia* (ed. A. Keast), 42 pp. Junk, The Hague.

Buscarlet, L.A. & Grenot, C. (1985) Utilisation des isotopes stables et radioactifs dans les études bioénergétiques des populations animales en milieu terrestre. *Acta Oecologica, Oecologia Generalis,* **6,** 105–134.

Congdon, J.D., Vitt, L.J., van Loben Sels, R.C. & Ohmart, R.D. (1982) The ecological significance of water flux rates in arboreal desert lizards of the genus *Urosaurus. Physiological Zoology,* **55,** 317–322.

Dufaure, J.P. & Hubert, J. (1961) Table de développement du Lézard vivipare: *Lacerta* (*Zootoca*) *vivipara* Jacquin. *Archives d'anatomie Microscopique et de Morphologie Expérimentale,* **50,** 309–327.

Grenot, C. (1981) Equilibres pondéral et hydrique du lézard saharien *Uromastix acanthinurus. Bulletin de la Société Zoologique de France,* **106,** 49–55.

Heulin, B. (1984) *Contribution à l'étude de la biologie des populations de* Lacerta vivipara*: stratégie démographique et utilisation de l'espace dans une population du massif forestier de Paimpont.* Third Cycle Thesis, University of Rennes.

Heulin, B. (1985a) Démographie d'une population de *Lacerta vivipara* de basse altitude. *Acta Oecologica, Oecologia Generalis,* **6,** 261–280.

Heulin, B. (1985b) Densité et organisation spatiale des populations du lézard vivipare *Lacerta vivipara* (Jacquin, 1787) dans les landes de la région de Paimpont. *Bulletin d'Ecologie,* **16,** 177–186.

Heulin, B. (1985c) Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara. Canadian Journal of Zoology,* **63,** 1773–1777.

Heulin, B. (1986) Régime alimentaire estival et utilisation des ressources trophiques dans trois populations de *Lacerta vivipara. Acta Oecologica, Oecologia Generalis,* **7,** 135–150.

Khodadoost, M., Pilorge, T. & Ortega, A. (1987) Variations de la densité et de la taille corporelle en fonction de l'abondance et de la composition du peuplement de proies dans trois populations de lézards vivipares du Mont Lozère. *Revue d'Ecologie* (*La Terre et la Vie*), **42,** 193–201.

Kobayashi, D., Mautz, W.J. & Nagy, K.A. (1983) Evaporative water loss: humidity acclimation in *Anolis carolinensis* lizards. *Copeia*, 1983, 701–704.

Lemire, M., Grenot, C. & Vernet, R. (1982) Water and electrolyte balance of free-living Saharan lizards, *Uromastix acanthinurus. Journal of Comparative Physiology,* **146,** 81–93.

Minnich, J.E. (1979) Reptiles. In *Comparative Physiology of Osmoregulation in Animals* (ed. G.M.O. Maloiy), pp. 391–641. Academic Press, London.

Nagy, K.A. (1982) Field studies of water relations. In *Biology of the Reptilia 12* (ed. C. Gans & F.H. Pough), pp. 483–501. Academic Press, London.

Nagy, K.A. (1983) Ecological energetics. In *Lizard Ecology: Studies of a Model Organism* (ed. R.B. Huey, E.R. Pianka & T.W. Schoener), pp. 24–54. Harvard University Press, Cambridge.

Nagy, K.A. & Costa, D.P. (1980) Water flux in animals: analysis of potential errors in the tritiated water method. *American Journal of Physiology,* **238,** 454–465.

Nagy, K.A., Huey, R.B. & Bennett, F. (1984) Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology,* **65,** 588–596.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Pilorge, T. (1982) Ration alimentaire et bilan énergétique individuel dans une population de montagne de *Lacerta vivipara*. *Canadian Journal of Zoology,* **60,** 1945–1950.

Pilorge, T. (1987) Density, size structure, and reproductive characteristics of three populations of *Lacerta vivipara* (Sauria, Lacertidae). *Herpetologica,* **43,** 345–356.

Siegel, S. (1956) *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.

Vernet, R., Lemire, M. & Grenot, C. (1987) Field studies of activity and water balance of a desert monitor *Varanus griseus* (Reptilia, Varanidae). *Journal of Arid Environments*, in press.

Vernet, R., Grenot, C. & Nouira, S. (1986) Renouvellement de l'eau et bilan énergétique journalier chez *Eremias olivieri* et *Acanthodactylus pardalis* (Sauria, Lacertidae) en milieu naturel, Iles Kerkennah (Tunisie). *Bulletin de la Société Herpétologique de France,* **36,** 13–19.

Xavier, F. & Gavaud, J. (1987) Oviparity-viviparity continuum in Reptiles: Physiological characteristics and relation with environment. In *Endocrine Regulation as Adaptive Mechanisms to the Environment* (ed. I. Assenmacher & J. Boissin), pp. 79–93. Centre National de la Recherche Scientifique, Paris.

Received 21 November 1986; revised 13 February 1987; accepted 17 February 1987